ANNALS OF CARNEGIE MUSEUM
Vol. 59, Number 1, Pp. 15–23 22 February 1990

ACTIVITY PATTERNS OF A CHIHUAHUAN DESERT SNAKE COMMUNITY

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Abstract

The effects of seasonal and yearly variation in soil temperature and precipitation on activity of a Chihuahuan Desert snake community were investigated over a four-year period in southcentral New Mexico. A direct, positive correlation exists between snake activity and both temperature and rainfall. There were significant differences, associated with differential responses to temperature and rainfall patterns, between viperids and other snakes in this community. The relationship between annual differences in relative activity and reproductive strategies among the component snake species is discussed.

Introduction

Community ecology remains one of the more intractable aspects of contemporary biology. A biological community may be most simply defined as an assemblage of species populations which occur together in space and time (Begon et al., 1986; Diamond and Case, 1986) and between which there is a potential for interaction (Strong et al., 1984). An explicit goal of community ecology is the marriage of life-history traits of component species to the evolutionary determinants of those traits. Realization of the importance of temporal variability in ecological parameters as an agent of selective change and community structure has recently been emphasized (Chesson, 1986; Davis, 1986; Partridge and Harvey, 1988). Among squamate reptiles, lizard community ecology is advancing apace (Huey et al., 1983; Pianka, 1986), but that of snakes has lagged (Toft, 1985; Vitt, 1987). The study of species diversity patterns is one way to gain insight into the structure of biological communities (Pielou, 1977; Ludwig and Reynolds, 1988). This study presents such data on a temperate-zone snake community in the Chihuahuan Desert of southern New Mexico, and attempts to relate variations in activity and abundance of component species to variations in proximate environmental factors and to differences in reproductive modes.

Methods

A census of a snake community was taken from 1975 through 1978 along a 25 km section of U.S. Highway 85 trending north-south between Radium Springs and Hatch in northwestern Doña Ana County, New Mexico. This highway was the main route between Las Cruces and Albuquerque until the completion of Interstate 25, and supported largely local traffic during the course of this study. The road sampled lies west of the Rio Grande, and within the current stabilized floodplain, except for a 1 km stretch which climbs over a northern spur of the Cedar Hills. The road is never more than 700

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Date submitted: 15 November 1988.

m from the river channel, and lies between 1200 and 1262 meters in elevation. The alluvial soil ranges from coarse to fine-textured. The climate is harsh, with freezing temperatures or below common during the winter and exposed surface soil temperatures commonly approaching 49°C during the summer. Ambient temperatures frequently span 20°C during a 24-hour period. Annual precipitation averages about 20 cm, and the majority falls sporadically during the summer as convective thundershowers of high intensity but brief duration. The study area has been settled by humans for at least 100 years, and presents a complex vegetational mosaic of cottonwood-Tamarisk, cultivated crops such as chile and cotton, and invading disclimax Chihuahuan Desert scrub dominated by *Larrea* and *Prosopis*. There are no distinct vegetational zones along the transect, although scattered remnants of historical riparian gallery forest still exist.

Sampling took place each year from April through September. A single round trip was taken each evening starting at dark. Snakes encountered were identified to species, and position along the transect (odometer distance from the starting point) recorded. Indices of activity calculated include the number of species per year, percent successful trips, number of snakes per trip and per 100 km of travel, and percent DOR (dead on road). Species diversity (Shannon's H′), and a measure of species equitability (% maximum H′) were also calculated. The non-viperid snakes, for purposes of analysis, were divided into two groups, rodent-eating colubrids (REC) and others. The REC were *Arizona elegans, Pituophis melanoleucus, Lampropeltis getulus* and *Elaphe subocularis*.

Monthly rainfall and soil temperature data were available from U.S. Weather Bureau stations in Hatch and at New Mexico State University in Las Cruces (Price, 1985). Soil temperatures were measured 10.16 cm below the ground surface (Dr. Norman Malm, School of Agricultural Sciences, New Mexico State University, personal communication). Soil temperature rather than air temperature was considered to be more directly relevant to snake activity, for perhaps obvious reasons, and was therefore used in this analysis. These weather stations bracket the study area to the north and south, respectively, and have been in operation since 1931 (Hatch, NM), 1858 (NMSU precipitation), and 1892 (NMSU temperature). A time span of 30 years prior to the study period (except 1957, for which data were unavailable) was selected for analysis in order to provide a time frame long enough to establish trends in these weather parameters that may be selectively important and at the same time provide sufficient mensural quality and resolution to be useful. All data were converted to metric units prior to analysis. Four matrices of six columns (monthly mean soil temperatures or monthly cumulative rainfall totals from April through September for each of the weather stations) by thirty rows (years) were thus created. Variation from year to year was assessed by adding the six values for each row to provide an overall mean soil temperature or cumulative rainfall total for each year, and then adding the resultant four columns to determine a mean and standard deviation for the 30-year baseline period. The soil temperature and rainfall figures for the study years were then compared to determine the deviation of each from the 30-year mean. Variation within years of these weather parameters during the study period was assessed by first adding the columns of each of the four matrices to provide monthly means for the 30-year baseline period. Variances for soil temperature and rainfall for each weather station during each study year were then calculated in the standard manner using the appropriate 30-year monthly mean as the subtrahend. Variances were tested for significant differences between years using F-tests.

RESULTS

Table 1 summarizes the data and indices calculated on a yearly basis. Eighteen snake species were observed during the course of this study. The year 1975 was a poor year for snakes compared to the remaining three years. The number of snakes per trip was significantly lower (multiple pairwise *t*-tests, 1975 vs. each of the other three years, $P < 0.005$; remaining pairwise comparisons, $P > 0.1$) and DOR percentage significantly higher ($\chi^2_{DOR} = 8.74$, df = 3, $P < 0.05$; $\chi^2_{DOR-1975} = 0.12$, df = 2, $P > 0.9$) in 1975 than in 1976–78. The percentage of successful trips, however, was not significantly different among any of the four years (χ^2 test).

Table 2 compares mean soil temperatures and cumulative rainfall during the six-month sampling period for each of the four study years to mean soil temperature and rainfall for the 30-year baseline period. Table 3 shows mean soil temperatures and rainfall for the study period and how variable these parameters were during each year. The timing of precipitation during the year rather than the annual accumulation is of greater biological relevance in this environment.

Table 1.—*Yearly summary of snakes encountered while road-collecting along a 25 km section of U.S. Highway 85 between Radium Springs and Hatch, Doña Ana County, New Mexico.*

	1975		1976		1977		1978		All	
	AOR	DOR	AOR	DOR	AOR	DOR	AOR	DOR	AOR	DOR
Crotalus atrox	4	11	52	33	15	19	43	32	114	95
Crotalus molossus	—	—	1	1	—	—	—	—	1	1
Crotalus viridis	—	—	4	0	0	1	0	1	4	2
Arizona elegans	0	1	13	5	2	2	1	0	16	8
Pituophis melanoleucus	0	8	16	26	1	7	1	8	18	49
Lampropeltis getulus	2	4	14	6	11	1	7	1	34	12
Elaphe subocularis	0	1	1	0	—	—	0	1	1	2
Hypsiglena torquata	3	2	4	4	5	0	2	0	14	6
Tantilla nigriceps	4	0	8	2	8	0	12	0	32	2
Gyalopion canum	—	—	0	1	—	—	—	—	0	1
Rhinocheilus lecontei	0	1	6	1	3	1	—	—	9	3
Sonora semiannulata	1	1	1	2	1	0	—	—	3	3
Thamnophis marcianus	1	0	1	1	2	1	—	—	4	2
Thamnophis sirtalis	—	—	—	—	0	1	0	1	0	2
Leptotyphlops sp.	1	0	—	—	2	0	2	1	5	1
Salvadora deserticola	—	—	0	5	0	1	0	1	0	7
Masticophis taeniatus	—	—	0	1	—	—	—	—	0	1
Masticophis flagellum	—	—	0	1	—	—	0	1	0	2
Totals	16	29	121	89	50	34	68	47	255	199
	45		210		84		115		454	
No. species	11		16		13		12		18	
No. trips	41		103		46		65		255	
% successful trips	63		76		76		77		74	
% DOR	64		42		41		41		44	
Snakes/trip	1.1		2.04		1.83		1.77		1.78	
Snakes/100 km	2.2		4.1		3.7		3.5		3.7	
H′	0.852		0.833		0.857		0.571		—	
% max. H′	82		69		77		53		—	

Although Table 2 does not show it at this scale of resolution, the entire six-month activity season during 1975 was colder and effectively drier than normal. Daily rainfall data (NMSU only) show that two-thirds of the total precipitation from mid-May through the end of August in 1975 fell on just three days and almost half of that (31% of the six-month total) fell on a single day towards the end of the season (August 22) (Price, 1985). Rainfall and soil temperatures were also significantly more variable during 1975 than any of the other three years (multiple pairwise *F*-tests, Table 3). We attribute the significantly greater percentage of DOR snakes during 1975 to the unusually cool season, which may have caused snakes that were active to remain on the pavement longer for thermoregulatory purposes (Klauber, 1939; Sullivan, 1981*a*) and thereby increased their chances of being killed by traffic.

Table 4 lists the population sample data and indices calculated on a monthly basis. Table 5 shows simple correlation coefficients between three indices from Table 4 (percent DOR; percent successful trips; snakes/100 km) and the monthly weather data from each station separately and for both stations combined. Snakes per 100 km of travel, a distance-independent index in this study, is significantly correlated with both previous and concurrent monthly precipitation and with previous, but not concurrent, monthly mean soil temperature. We interpret this

Table 2.—*Mean and standard deviation for monthly mean soil temperature and mean cumulative rainfall from April through September for the 30-year period, 1944–74. Rainfall figures for 1975–78 are 6-month accumulations, April–September. Figures in parentheses are the number of standard deviations above or below the 30-year mean that would encompass the value indicated.*

	Soil temperature (°C)		Precipitation (cm)	
	Hatch, NM	NMSU	Hatch, NM	NMSU
1944–74	22.16 ± 0.51	22.50 ± 0.58	15.65 ± 5.36	12.94 ± 5.64
1975	20.43 (−4)	21.23 (−3)	24.59 (+2)	14.58 (+1)
1976	21.49 (−2)	22.06 (−1)	13.39 (−1)	13.34 (+1)
1977	22.60 (+1)	22.87 (+1)	13.67 (−1)	16.56 (+1)
1978	22.22 (+1)	22.96 (+1)	16.94 (+1)	21.67 (+2)

to suggest that snake activity in this community depends to some degree upon regional substrate warming, and thus a critical ground temperature threshold must be reached and maintained before snakes become generally and widely active. Percent successful trips, which is a distance-dependent index, is significantly correlated with both previous and concurrent monthly mean soil temperature and with concurrent, but not previous, monthly precipitation. We interpret this to suggest that once the ground is warm enough in this environment to support snake activity, rainfall stimulates snakes to move.

Species diversity indices from Table 1 were recalculated and tested for significant comparisons based on the method of Hutcheson (1970). Results (Table 6) demonstrate that 1978 was the least diverse of the four years of this study. The difference is particularly significant when compared with the other two "good" years for snakes, 1976 and 1977. This lowered diversity was due to the dominance of *Crotalus* in the 1978 sample ($\chi^2_{Crotalus/\mathrm{other}} = 22.13$, df = 3, $P < 0.001$; $\chi^2_{Crotalus/\mathrm{other}\text{-}1978} = 1.53$, df = 2, $P > 0.25$) and not to differences in the proportion of REC to non-REC in that sample ($\chi^2_{\mathrm{REC/nonREC}} = 8.18$, df = 3, $P < 0.05$; $\chi^2_{\mathrm{REC/nonREC}\text{-}1978} = 6.22$, df = 2, $P < 0.05$). In fact, REC contributed disproportionately to the species diversity index only in 1976 ($\chi^2_{\mathrm{REC/nonREC}\text{-}1976} = 0.18$, df =

Table 3.—*Yearly means and variances for the weather data during the sample period, April–September. Variances were calculated based on the monthly deviations from the respective 30-year averages. F-values result from pairwise comparisons between sample variances.* ** *denotes P* < 0.05.

	Soil temperature (°C)				Precipitation (cm)			
	Hatch, NM		NMSU		Hatch, NM		NMSU	
	Mean	s^2	Mean	s^2	Mean	s^2	Mean	s^2
1975	20.43	3.60	21.23	2.58	4.10	20.17	2.43	2.85
1976	21.49	0.66	22.06	0.49	2.23	1.40	2.22	2.39
1977	22.60	0.93	22.87	0.89	2.28	0.71	2.76	2.42
1978	22.22	0.84	22.96	1.41	2.82	5.26	3.61	6.54
F-values	75 vs 76**		75 vs 76**		75 vs 76**		75 vs 76 NS	
	75 vs 77 NS		75 vs 77 NS		75 vs 77**		75 vs 77 NS	
	75 vs 78**		75 vs 78 NS		75 vs 78 NS		75 vs 78 NS	
	76 vs 77 NS		76 vs 77 NS		76 vs 77 NS		76 vs 77 NS	
	76 vs 78 NS		76 vs 78 NS		76 vs 78 NS		76 vs 78 NS	
	77 vs 78 NS		77 vs 78 NS		77 vs 78**		77 vs 78 NS	

Table 4.—*Monthly summary of snakes encountered while road-collecting along a 25 km section of U.S. Highway 85 between Radium Springs and Hatch, Doña Ana County, New Mexico, during the years 1975–78.*

	April		May		June		July		Aug.		Sept.	
	AOR	DOR	AOR	DOR	AOR	DOR	AOR	DOR	AOR	DOR	AOR	DOR
Crotalus atrox	1	2	9	6	12	6	22	23	50	39	20	19
Crotalus molossus	—	—	—	—	1	0	—	—	0	1	—	—
Crotalus viridis	—	—	0	1	1	0	—	—	1	0	2	1
Arizona elegans	1	0	5	2	4	1	0	1	5	3	1	1
Pituophis melanoleucus	1	1	5	5	0	8	0	6	3	9	9	20
Lampropeltis getulus	1	0	2	1	6	1	16	5	5	2	4	3
Elaphe subocularis	—	—	—	—	—	—	1	1	—	—	0	1
Hypsiglena torquata	0	1	1	0	4	1	7	1	1	1	1	2
Tantilla nigriceps	2	0	7	0	5	0	12	1	5	1	1	0
Gyalopion canum	—	—	—	—	—	—	0	1	—	—	—	—
Rhinocheilus lecontei	1	0	1	1	4	1	1	0	2	1	—	—
Sonora semiannulata	—	—	0	1	—	—	2	1	1	1	—	—
Leptotyphlops sp.	—	—	1	1	—	—	3	0	—	—	1	0
Thamnophis marcianus	—	—	—	—	2	0	—	—	2	2	—	—
Thamnophis sirtalis	—	—	—	—	0	1	0	1	—	—	—	—
Salvadora deserticola	0	2	0	1	0	2	—	—	0	2	—	—
Masticophis taeniatus	—	—	—	—	—	—	0	1	—	—	—	—
Masticophis flagellum	—	—	0	1	0	1	—	—	—	—	—	—
Totals	7	6	31	20	39	22	64	42	75	62	39	47
	13		51		61		106		137		86	
No. species	8		12		13		13		12		9	
No. trips	13		40		45		61		57		38	
% successful	54		65		76		77		77		82	
% DOR	46		39		36		40		45		55	
Snakes/trip	1.0		1.3		1.4		1.7		2.4		2.3	
Snakes/100 km	2.0		2.5		2.7		3.5		4.8		4.5	
H′	0.866		0.880		0.950		0.782		0.604		0.621	

Table 5.—*Simple correlation coefficients between three indices of snake activity from Table 3 and the weather data from Price (1985; summarized in Table 2). * denotes P(r) < 0.05, ** P(r) < 0.01.*

		% DOR	% Successful days	Snakes/km
Previous monthly precipitation	Hatch, NM	0.632	0.561	0.920**
	NMSU	0.743	0.740	0.894*
	Both	0.727	0.689	0.957**
Concurrent monthly precipitation	Hatch, NM	0.511	0.851*	0.829*
	NMSU	0.598	0.793	0.994**
	Both	0.571	0.852*	0.938**
Previous monthly mean temperature	Hatch, NM	0.256	0.925**	0.918**
	NMSU	0.270	0.920**	0.923**
	Both	0.263	0.922**	0.920**
Concurrent monthly mean temperature	Hatch, NM	−0.311	0.823*	0.584
	NMSU	−0.288	0.829*	0.598
	Both	−0.299	0.826*	0.591

2, $P > 0.9$). These results are supported by the species equitability measures (Table 1).

Discussion

Roadriding has been shown to be an effective technique for sampling snake communities in desert environments (Klauber, 1939; Pough, 1966; Sullivan, 1981*b*; Reynolds, 1982; Reynolds and Scott, 1982; Price, 1985). Data gathered during this study demonstrate that 1975 was a poor year for snake activity relative to three other years, and that the apparent community structure was influenced by the dominance of *Crotalus* in 1978. These two salient results can best be explained as the outcome of a combination of environmental and life-history factors.

Climatic variables such as temperature and rainfall have a major impact upon snake activity patterns (Gibbons and Semlitsch, 1987; Lillywhite, 1987). Reynolds (1982) found a sharp peak in snake activity during August in northeastern Chihuahua, Mexico, significantly correlated with the previous month's precipitation. He attributed this to the effect of rainfall on primary productivity, providing an increased abundance of prey after a lag time. Results presented here show a broader peak in activity from July through September. Temperature and rainfall in our community act directly to promote snake activity, and not apparently through influence on intermediate trophic levels. The contrast between these two communities may partly be attributable to differences in habitat. The transect sampled by Reynolds (1982) traverses open desert, whereas the transect sampled in this study is along a riparian and agricultural corridor. The constant availability of water due to the position of the underlying water table and agricultural irrigation likely render the proximate influence of rainfall on primary productivity less important.

Reynolds and Scott (1982) showed that prey differences among snake species and habitat differences among both snakes and their prey are important determinants of structure in a Chihuahuan Desert snake community. Toft (1985) emphasized the importance of the food dimension in resource partitioning among sympatric snake species. As there appear to be no major habitat breaks or transitions along the study transect, neither habitat of snakes nor that of their prey is

Table 6.—*Yearly species diversity indices and tests for significant differences based on the method of Hutcheson (1970).*

	H′ (ln)	E(H′)	var (H′)
1975	1.96	1.77	0.058
1976	1.92	1.88	0.015
1977	1.97	1.87	0.035
1978	1.31	1.24	0.019
	df	t	*P*
75 vs 76	70	0.396	NS
75 vs 77	97	0.31	NS
75 vs 78	76	1.93	<0.1
76 vs 77	160	0.059	NS
76 vs 78	275	3.48	<0.001
77 vs 78	165	2.70	<0.01

presumed to be an important factor in the differences in abundance and diversity found in this snake community. Both *Crotalus* and the REC portions of the community studied are presumed to share the same food resource, although evidence for this is anecdotal and circumstantial (Klauber, 1972; Shaw and Campbell, 1974; Stebbins, 1985; personal observations). Food resource partitioning is not, therefore, considered to be of primary importance here either.

The proximate effects of temperature, precipitation, and food, taken singly or together, do not appear to account completely for the community activity patterns seen during this study. Species populations in a fluctuating environment should track the long-term averages of selectively important environmental parameters as precisely as possible (Templeton, 1982; Lande, 1988). Given that each snake species has an optimal physiological activity range, largely mediated by temperature and moisture conditions (Lillywhite, 1987), a climatically variable year may suppress activity relative to a more average year. It appears that 1975 was such a threshold year in this study; 1975 was a poor year for snake activity, for all species, relative to 1976–78.

Species diversity in 1978 was significantly lower than the previous three years due to an increase in the proportion of *Crotalus* in the sample. This increase was due to activity from August onward (Table 4) and largely represents young of the year (personal observation). There are distinct differences in the reproductive strategies adopted by the various species in this community. *Crotalus* are live-bearers whereas the REC in this study are oviparous. An examination of the weather data presented here and elsewhere (Price, 1985) indicates that 1978 was the climatically next most variable year to 1975. In fact, the REC contribute disproportionately to the community structure only in 1976, which appears to be the most climatically equitable of the four years. Although the adaptive value of viviparity and its influence on the zoogeography of squamate reptiles has been well discussed (Neill, 1964; Tinkle and Gibbons, 1977; Shine and Berry, 1978; Shine and Bull, 1979; Shine, 1983, 1985), not enough attention has been paid to the direct influence of variable climatic parameters on the life-history stages of snake populations, and to how individual species responses to such parameters might help shape community structure (Lillywhite, 1987). This study suggests that while proximate climatic factors have a direct and significant impact on an observed community of snakes in the Chihuahuan Desert, the component species respond differently to variations in these factors, and these responses cannot totally be accounted for by differences in resource utilization profiles. The precise temperature and moisture regimes necessary for reptile eggs to develop properly and hatch are well known (Packard et al., 1977; references in Hubert, 1985; Saint Girons, 1985; and Shine, 1985). The numerical predominance of *Crotalus* in this and other studies may be explained in part by their ability to sequester their "eggs" away from the potentially debilitating vagaries of the environment.

Acknowledgments

This study resulted from master's thesis research by the senior author. Field work was supported by the Biology Department, New Mexico State University, and by the senior author. Data analysis was supported by Personal Services Contract No. 519-72-07 from the Endangered Species Program, New Mexico Department of Game and Fish, to the senior author. Rita Lawler contributed materially in the initial stages of the analysis. Wirt Atmar, Marsha Conley, Arthur Dunham, John Hubbard, David Lightfoot, Jack McCoy, Eric Pianka, Robert Reynolds, Norm Scott, Laurie Vitt and two anonymous reviewers critically read various drafts of the manuscript.

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